The Anatomy and Histology of the Male Reproductive System of the Legionary Ant, *Neivamyrmex harrisi* (Haldeman) (Hymenoptera: Formicidae)[1]

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Abstract This paper presents the first description of the anatomy and histology of the male reproductive system for this doryline ant. Anatomical descriptions of the eighth and ninth sterna are included. The male system consists of the testes, the vasa deferentia, the accessory glands and ducts, the bound accessory gland duct, the ejaculatory duct, and the genitalia. The testes, situated in the third gastral segment, lie between the proximal arms of the U-shaped vasa deferentia and are covered with a single capsule. Each testis has about 22–25 tubular follicles. The vasa deferentia are packed with spermatozoa, and a granular mass fills their posterior ends. The coiled accessory glands lie on either side of the fourth gastral segment, and they contain a dense, homogeneous, basophilic secretion. Their ducts meet medially and become surrounded with circular muscle to form the bound accessory gland duct; two lumina are present throughout the length of the bound accessory gland duct. At the posterior end of this duct, the two lumina unite into one to form the ejaculatory duct in which a sclerotized wedge is located. The position of the wedge in the duct and the unicellular glands at the posterior end of the duct are described. The ejaculatory duct opens on the dorsal, posterior region of the aedeagal bladder, which empties between the inner valves of the genitalia. The aedeagal bladder contains a granular, basophilic secretion. Three pairs of valves and a basal ring constitute the genitalia. Sperm gutters are present on the inner valves. Comparisons are made with the male systems for two dorylines previously reported, *Dorylus labiatus* and *Eciton hamatum,* which place *Neivamyrmex* anatomically closer to *Eciton* than to *Dorylus.*

This paper presents the first description of the anatomy and histology of the male reproductive system of the doryline ant, *Neivamyrmex harrisi* (Haldeman). Descriptions of the external genitalia and ventral terminal segments, eight and nine, are also included.

A comparative survey of the male reproductive systems for the formicid genera and species reported in the literature has been made (Forbes, 1954). Although these systems have been described for only a few genera, distinguishing characteristics have been observed for each genus.

The male systems have been described for only two other doryline ants, the Old World *Dorylus labiatus* (Mukerjee, 1927) and the New World *Eciton hamatum* (Forbes, 1958). In this study, *Neivamyrmex* is compared with *Eciton* and *Dorylus*. Again, differences are revealed; these place *Neivamyrmex* anatomically closer to *Eciton* than to *Dorylus*.

The male ants for this study were collected during July and August of 1956 at the Southwestern Research Station of the American Museum of Natural

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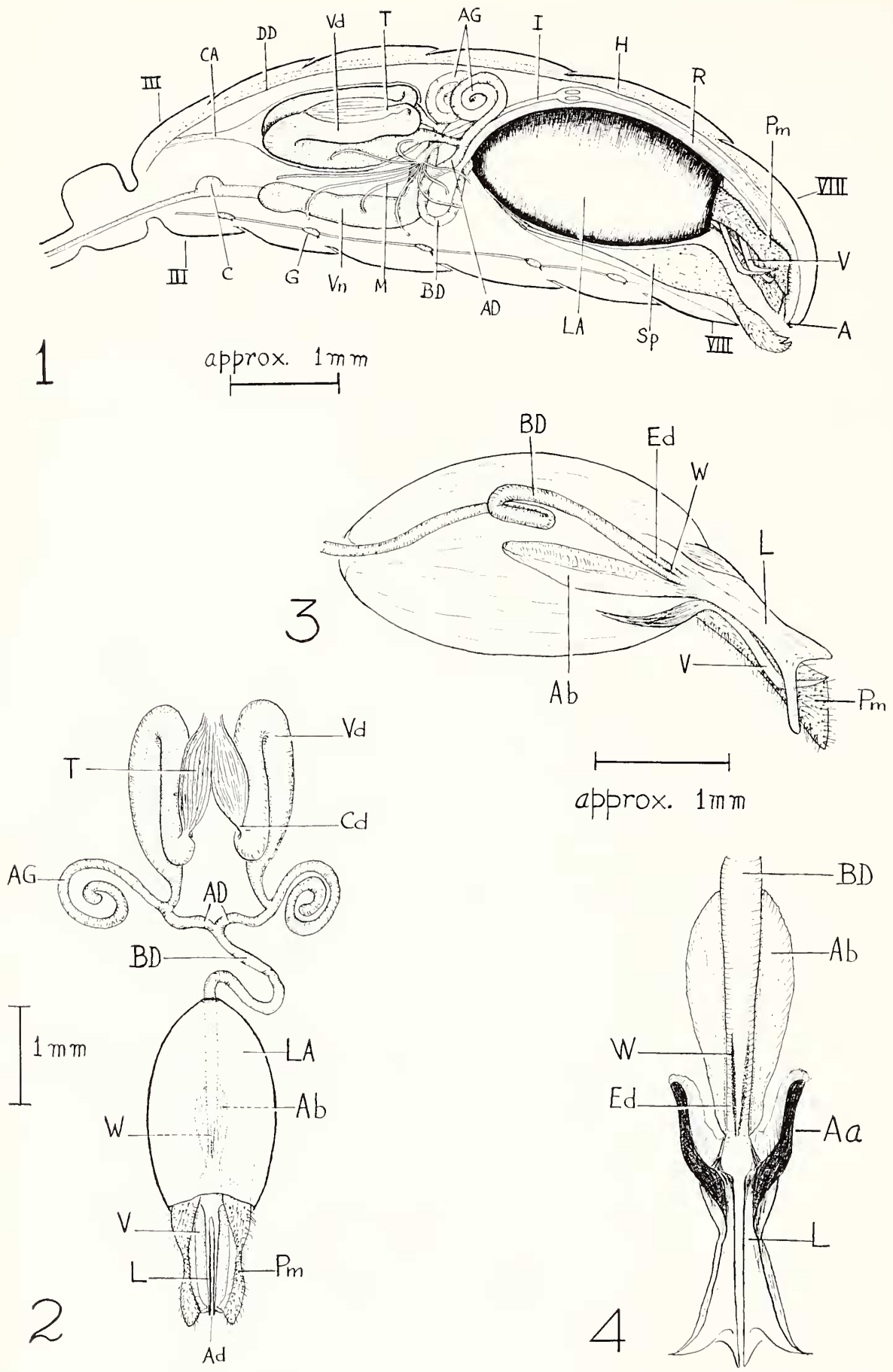

FIG. 1. Diagram of lateral dissection of the gaster of the male of *Neivamyrmex harrisi.*

FIG. 2. Diagram of dorsal view of male reproductive system and external genitalia. Dotted lines indicate organs within the basal ring or lamina annularis.

FIG. 3. Diagram of lateral dissection of the lamina annularis to show position of the bound

History in Cave Creek Canyon, Arizona by Doctors Mont Cazier, then the Director of the Station, and T. C. Schneirla, of the Museum. The specimens were males on nuptial flight since they were collected at night from light traps and from lighted, white sheets set up expressly to collect night-flying insects. About half of the male ants were fixed and stored in 70 per cent alcohol plus 1 per cent glycerine. The rest were fixed in Bouin's fluid for 12 hours and then stored in 70 per cent alcohol plus 1 per cent glycerine. M. R. Smith, of the United States Department of Agriculture, Entomology Research Division, determined the specimens.

Reproductive systems were dissected from the gasters, stained with borax carmine, and prepared as whole mounts for study. Whole gasters were dehydrated in ethyl alcohol, cleared in xylol, and embedded in 56–58 degree Fisher's tissue-mat for sectioning. Transverse and longitudinal sections were cut at 8 and 10 micra. The sections were stained with Harris' hematoxylin and counterstained with triosin.

The drawings were made from the whole mounts and the sections with the aid of a Bausch and Lomb Trisimplex microprojector.

ANATOMY OF THE REPRODUCTIVE SYSTEM

The reproductive system of the male *Neivamyrmex harrisi* (Haldeman) consists of the testes and vasa efferentia, the vasa deferentia, the accessory glands, the ducts of the accessory glands and the bound accessory gland duct, the ejaculatory duct, the aedeagal bladder, and the external genitalia (Figs. 1 and 2).

The testes are located in the median, posterior region of the third gastral segment, and they lie dorsomedially between the proximal ends of the apposed, prominent arms of the vasa deferentia (Fig. 2). Each testis is composed of about 22–25 slender, thin-walled tubules, the testicular follicles. Each testicular follicle ends in a short, constricted portion, a vas efferens. The vasa efferentia are collected into a common duct, which opens into the first part of the vas deferens. The testes are enclosed within a single, testicular capsule which is richly supplied with tracheae.

The vasa deferentia are thick-walled, prominent, U-shaped tubes. The arms of each U are approximately equal in length. The first part of the proximal arm of each vas deferens is usually bent at right angles and may be slightly dilated. It continues anteriorly through the length of the third gastral segment and to the posterior portion of the second segment. It then loops ventrally and becomes the distal arm, which continues back and lies ventral to the proximal arm. The

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accessory gland duct, the ejaculatory duct with wedge, and the aedeagal bladder; left genitalic valves removed.

Fig. 4. Diagram of dorsal view of the terminal portion of the reproductive system; inner genitalic valves in position.

dorsal or proximal arm may be wider in diameter than the ventral or distal arm (Fig. 18). The posterior ends of these distal arms of the vasa deferentia constrict gradually and open into the ducts of the accessory glands in the first portion of the fourth gastral segment. The vasa deferentia are covered by a capsule, which appears to be a continuation of the testicular capsule. This capsule is extended anteriorly from the testes and the vasa deferentia, and it is attached to the underside of the dorsal diaphragm in the first gastral segment (Fig. 1).

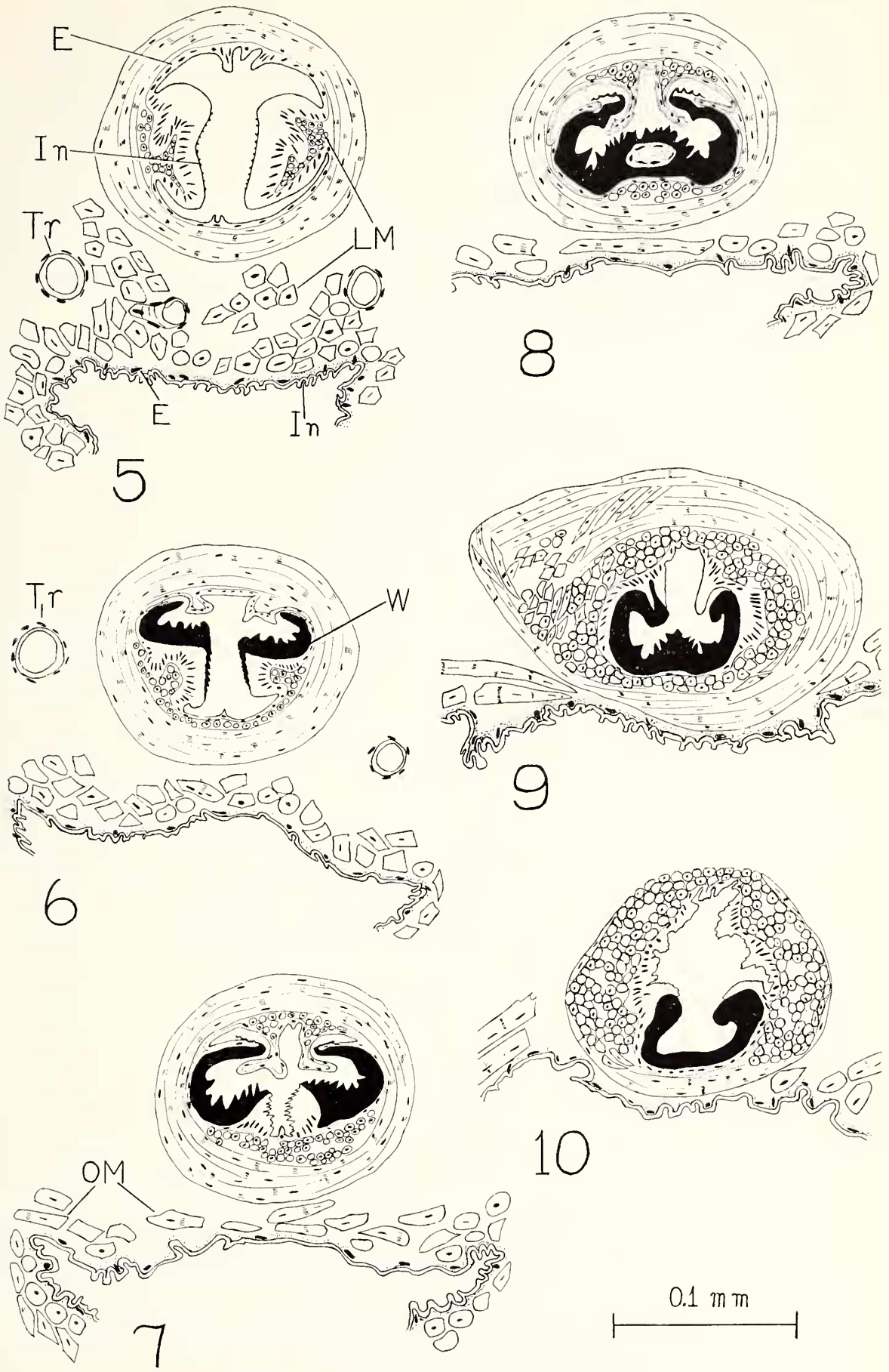
The accessory glands are tightly coiled tubes situated on either side of the intestine in the fourth gastral segment. They lie dorsolaterad of the vasa deferentia and just in front of the large cup-shaped lamina annularis or basal ring of the external genitalia. When uncoiled, each gland measures about 3.5 mm in length. The proximal end of each gland proceeds medially to meet the one from the other side. Before they meet, each is joined by the constricted end of a vas deferens. The section of the duct between this junction with the vas deferens and the meeting of the two ducts is called the accessory gland duct (Fig. 2). As the ducts of each gland meet, they are bound together by circular muscle. From here to the end of the system there appears to be one tube. However, histological sections of the duct reveal two lumina (Fig. 23), except at the end. This bound accessory gland duct is approximately 5 mm in total length and lies in the middle of the gaster just below the intestine. It bends anteroventrally, then proceeds posteriorly and dorsally to pass through the dorsal, anterior opening of the lamina annularis or basal ring of the external genitalia. Within the lamina annularis, the bound accessory gland duct makes a small loop or a sharp, S-shaped bend. It terminates on the dorsal, posterior end of the aedeagal bladder (Fig. 3).

Shortly before opening into the aedeagal bladder, the two lumina of the bound accessory gland duct join into a single lumen, which forms the ejaculatory duct. Here, in the lumen of the posterior portion of this ejaculatory duct, is located a slender, sclerotized wedge (Figs. 3 and 4). This wedge is approximately 0.6 mm in length and 0.08 mm in width at the anterior ends of the arms.

The aedeagal bladder is a thick-walled, boat-shaped sac, wider dorsally and constricted ventrally. It lies beneath the posterior end of the bound accessory gland duct and the ejaculatory duct within the lamina annularis (Figs. 3 and 4). The muscle wall is thicker at the anterior end of the bladder than at its posterior ends. The bladder opens posteriorly between the inner valves and the external genitalia.

EXTERNAL GENITALIA AND VENTRAL TERMINAL SEGMENTS

The external genitalia of *Neivamyrmex harrisi* (Fig. 1) is retracted and lies in a large cavity beneath the rectum and the anus within the last few gastral segments. This is typical for the dorylines (Borgmeier, 1955; Forbes, 1958);

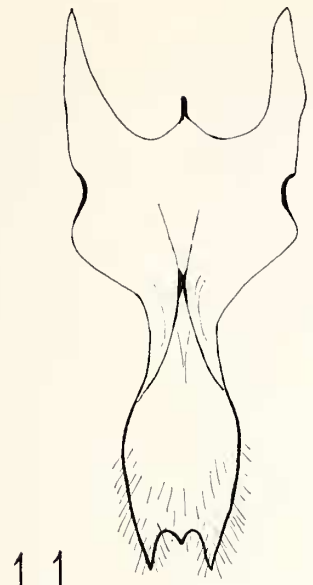


Figs. 5–10. Diagrams of series of cross sections of the ejaculatory duct and the wedge together with the dorsal surface of the underlying aedeagal bladder. In Figs. 5 and 6, the muscle layer of the dorsal surface of the aedeagal bladder is thicker than indicated.

often, only the posterior tip of the ninth sternum, the subgenital plate, projects from the end of the gaster. The genitalia of this ant conforms to the formicine pattern, which consists of three pairs of valves surrounded at their anterior ends by the basal ring or lamina annularis (Clausen, 1938; Snodgrass, 1941; Krafchick, 1959).

The lamina annularis is an elongated cup-shaped or tubular-shaped segment, which is moderately sclerotized throughout (Figs. 1 and 2). The outer valves are divided into two regions: the proximal region or lamina parameralis is somewhat globular in shape, and the distal region or paramere is blade-like. The posterior margin of the paramere is obliquely truncated. This outer valve is moderately sclerotized with the paramere slightly less so. Numerous, long slender hairs cover the paramere (Fig. 13). The middle valves or laminae volsellares are thin, tubular segments arranged in a shallow S-curve. The small, spheroidal-shaped proximal end of this valve is attached to the posteromedian surface of the lamina parameralis of the outer valve, and the sharply pointed distal end is directed dorsally. The volsellares are moderately sclerotized and devoid of hairs. The inner valves consist of a pair of laterally compressed plates, the laminae aedeagales, which are slightly less sclerotized than the outer and the middle valves (Figs. 4 and 14). They are joined along their dorsal margins by a weakly sclerotized membrane, the spathe. These inner valves are narrower anteriorly than posteriorly. At the posterior end the valve is divided into a dorsal and a ventral lobe. The dorsal lobe is round and blunt in shape, but the ventral one is extended into a laterally projecting hook. Along the upper portion and on the inner surface of each valve, there is a shallow groove, the sperm gutter, which extends from the anterior end almost to the posterior tip (Figs. 16 and 17). The aedeagal apodeme is located on the outer wall and is more sclerotized than the plate of the valve. It consists of two parts, a diagonal extension which supports the valve and a lower anterior portion for the attachment of muscles. The inner valves are devoid of hairs.

The ninth sternum or subgenital plate (Fig. 11) has a broad, anterior half and a narrow, ventrally depressed, somewhat spoon-shaped posterior half. The posterior portion is strongly sclerotized, while the anterior portion is much less so. There are three anterior extensions on the forward margin, with the middle one shorter and smaller than the lateral ones. The posterior margin terminates in three teeth-like projections; again the middle one is shorter than the lateral ones. Short hairs are present around the posterior end. The eighth sternum (Fig. 12) is a broad, slightly rectangular-shaped segment with a V-shaped cleft on the posterior margin. The cleft extends about one-third into the segment, and there is a slight ventral depression on either side of it. The whole segment is moderately sclerotized, with the posterior third more weakly so. A double row of hairs runs along the midline anterior to the cleft, and numerous, short hairs cover the posterior half of this segment.



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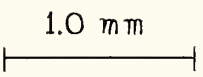

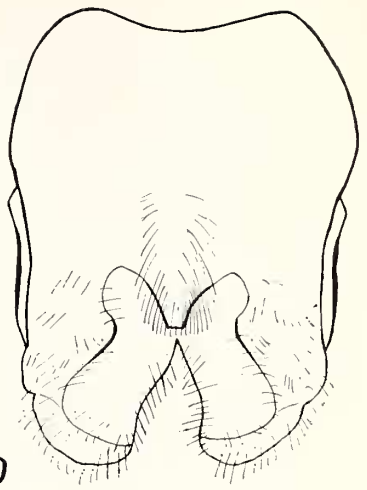

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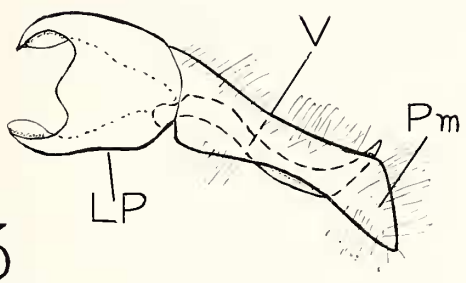

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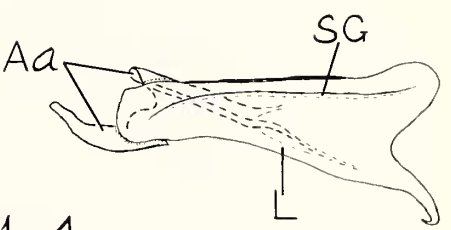

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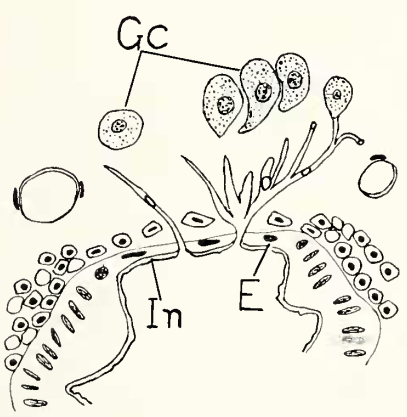

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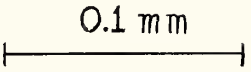

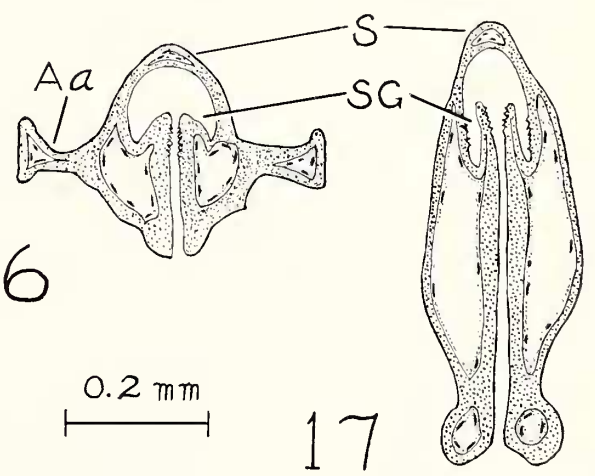

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FIG. 11. Diagram of ventral view of IXth abdominal sternum or subgenital plate.

FIG. 12. Diagram of ventral view of VIIIth abdominal sternum.

FIG. 13. Diagram of lateral view of the outer and middle genitalic valves.

FIG. 14. Diagram of median view of an inner genitalic valve.

FIG. 15. Diagram of the unicellular glands and dorsal wall of the ejaculatory duct near its opening into the aedeagal bladder.

FIG. 16. Diagram of cross section of inner genitalic valves through the anterior third to show the sperm gutters.

FIG. 17. Diagram of cross section of inner genitalic valves through the posterior third to show the sperm gutters.

HISTOLOGY OF THE REPRODUCTIVE SYSTEM

The follicles which make up the testes are slender, thin-walled tubules. In sectional view, they appear polyhedral or irregular in shape, and a few are round (Figs. 18 and 19). The cells which compose the walls of the testicular follicles are flat, polyhedral-shaped cells built on a distinct basement membrane. Their cytoplasm is granular and acidophilic in staining reaction, and the nuclei are irregular in shape and compact. The free surfaces of the cells are irregular, and short, protoplasmic projections or strands of granules extend into the lumina of the follicles. Some follicles have a distinct lumen packed with granules; in others, however, the lumina are indistinct. A few, fine muscle fibers intertwine external to the basement membranes of the follicles. Usually spermatozoa are not found in the follicles nor are cell divisions apparent. These follicles are not functioning and may be disintegrating. However, in sections of two males, but in only one testis of each, clusters of spermatozoa were observed toward the bases of a few follicles. In these testes, the cells of the follicular walls were smaller and more numerous, the nuclei of the cells were more oval in shape, and the chromatin was less compact.

The cells of the vas efferens are low, cuboidal in shape, with acidophilic cytoplasm and compact, irregularly-shaped nuclei. The lumen of some of the vessels appears indistinct and contains some acidophilic granules; in others, no lumen is evident. The vasa efferentia are collected into a short, narrow, common duct, which is composed of low cells built on a distinct basement membrane. The epithelium of the common duct may be transversely folded. Some of the cells have very fine cytoplasmic projections which extend into the lumen of the duct. The lumen of the first part of the duct is often filled with an acidophilic secretion. Spermatozoa are present in the lumina of the common ducts of the two specimens whose testes had spermatozoa in the follicles. This common duct continues into the proximal arm of the vas deferens (Fig. 20). The muscle fibers which are situated around the bases of the testicular follicles are continued obliquely around the vasa efferentia and the common duct.

At first glance, the capsule which surrounds the testes and the vasa deferentia appears fibrous in nature and contains many fusiform nuclei. Upon closer examination, however, the fibers appear to be composed of fine, parallel fibrils, and, in cross section, many of the fibrils appear tubular (Fig. 19). This may mean that the capsule is composed of bundles of branching and anastomosing tracheae and tracheoles. Granular material, similar to the granular material within the follicles, is scattered or may be clustered between the follicles. In a few sections, this granular material is divided into fairly large polygonal areas by what appears to be incomplete membranes. The sizes and shapes of these polygonal

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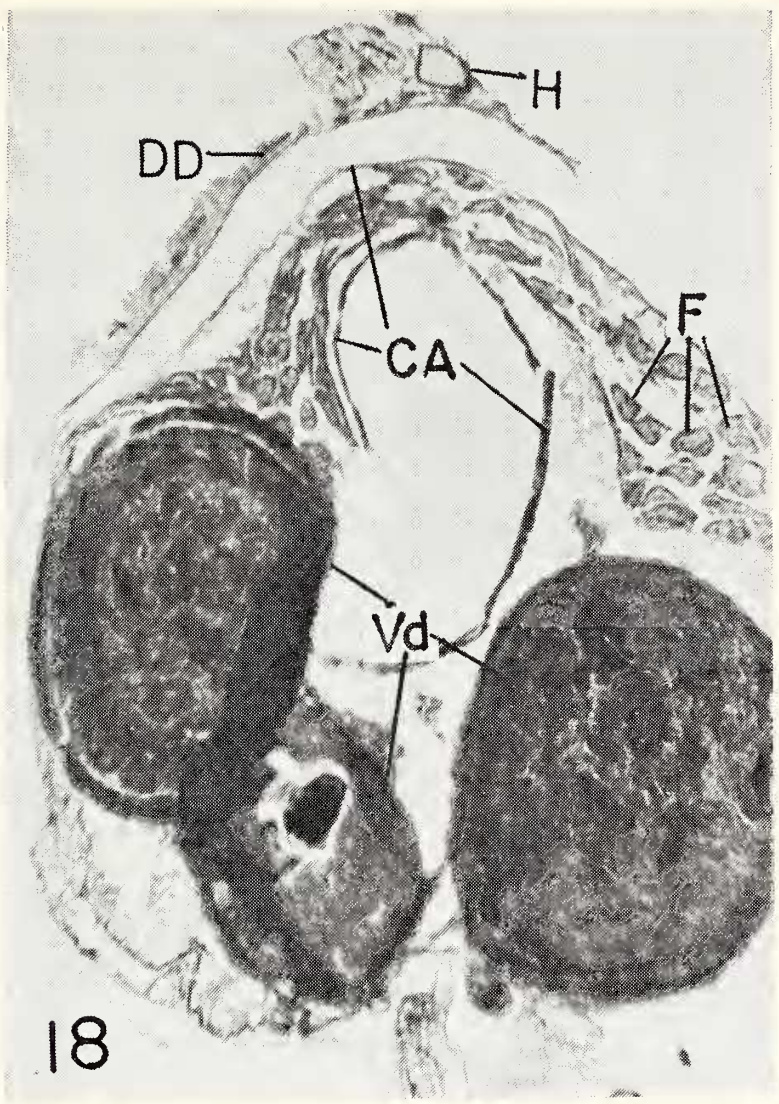
FIG. 18. Photomicrograph of transverse section of testes and vasa deferentia. × 450.
FIG. 19. Photomicrograph of testis and vas deferens. × 1,935.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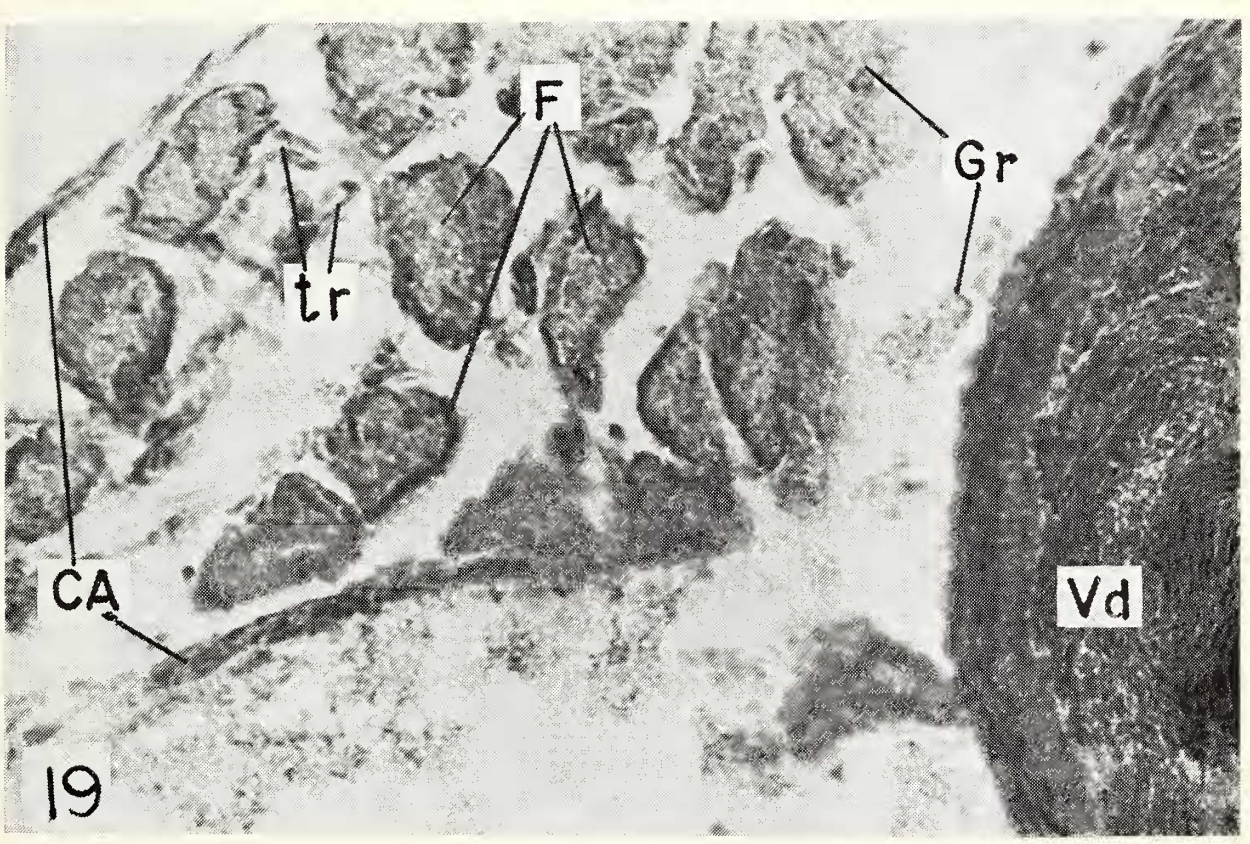
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areas suggest that they might be disintegrating fat cells or disintegrating follicles.

In the first part of the proximal arm of the vas deferens, the epithelial cells are quickly increased in height to become columnar-shaped and then are increased somewhat in width. A distinct basement membrane underlies the epithelium throughout. The cytoplasm of the epithelial cells of this organ is acidophilic. The nuclei in the columnar epithelium are compact, spherical in shape, and basally located. The free surfaces of these cells are irregular, some are undulating, and others may have very fine projections which extend into the lumen. A single layer of small, obliquely arranged muscle fibers surrounds the epithelium. The lumen of this first portion is usually filled with a granular secretion mass which contains a few spermatozoa. The wider, epithelial cells line almost the entire length of the vas deferens (Figs. 18, 19, and 20). These cells have flattened, ellipsoidal-shaped nuclei which are arranged with their long axes parallel to the basement membrane. The free surfaces of these cells are smooth. The muscle fibers are increased in number and are arranged into two layers, an inner circular layer and an outer longitudinal layer. The lumen is packed with spirally arranged clusters of spermatozoa, and, in some sections, the spermatozoan heads seem to be embedded in the free surface of the cells. In the distal region the epithelial cells become cuboidal-shaped. The flattened or ellipsoidal-shaped nuclei still have their long axes parallel with the basement membrane. The lumen here is also packed with spermatozoa. The muscle layers outside the epithelium are a little thicker. As the short, constricted region of the vas deferens is reached, the epithelium again changes to columnar-shaped cells, and the surrounding muscle fibers are oblique in direction. The lumen of this constricted region is filled with an acidophilic, granular material and a few, scattered spermatozoa.

The simple epithelial cells of the accessory glands are built on a basement membrane (Fig. 21). These cells vary in height in different regions from very high columnar-shaped cells all the way down to squamous-shaped cells. The cytoplasm of the cells is filled with fine, basophilic granules, and the free surface of the cells is often irregular. The lumen of the accessory glands contains a dense, homogeneous, basophilic secretion which appears to originate from the free surface of the cells. This secretion must be viscous in nature because it has a rather solid, band-like or ribbonlike appearance in the gland lumen. Usually, the secretion assumes a smooth, ribbon shape, which follows the contour of the lumen. However, examination of stained and cleared whole mounts of the glands in which the secretion is also prominently colored shows the band of secretion

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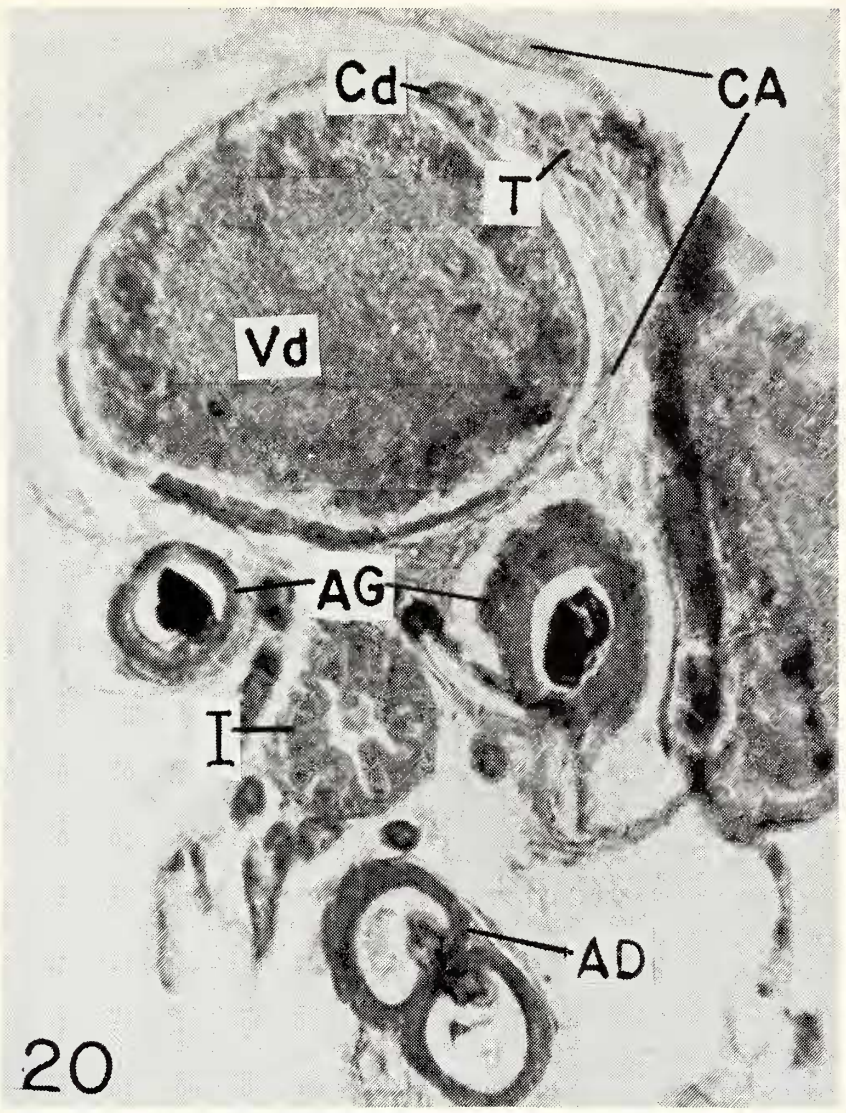
Fig. 20. Photomicrograph of transverse section of proximal arm of vas deferens, accessory glands, and accessory gland ducts. × 450.

Fig. 21. Photomicrograph of transverse section of an accessory gland with secretion arising from epithelium on lower surface. × 1,935.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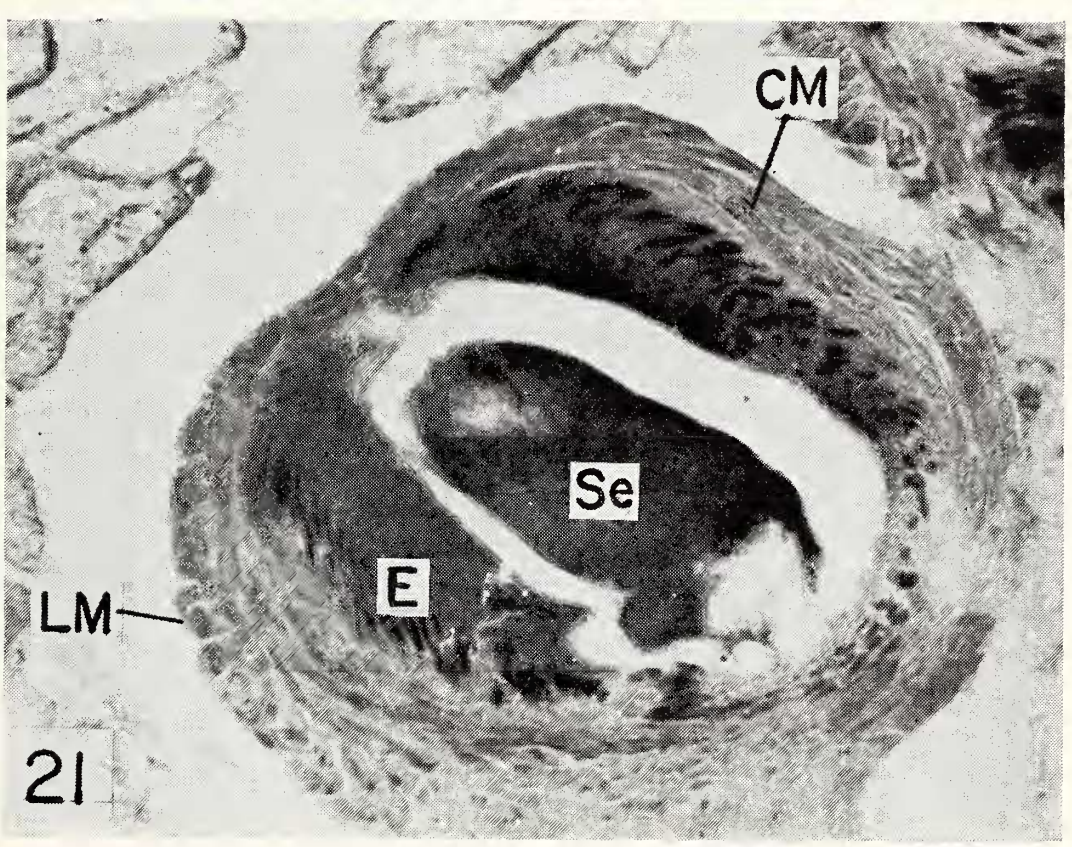
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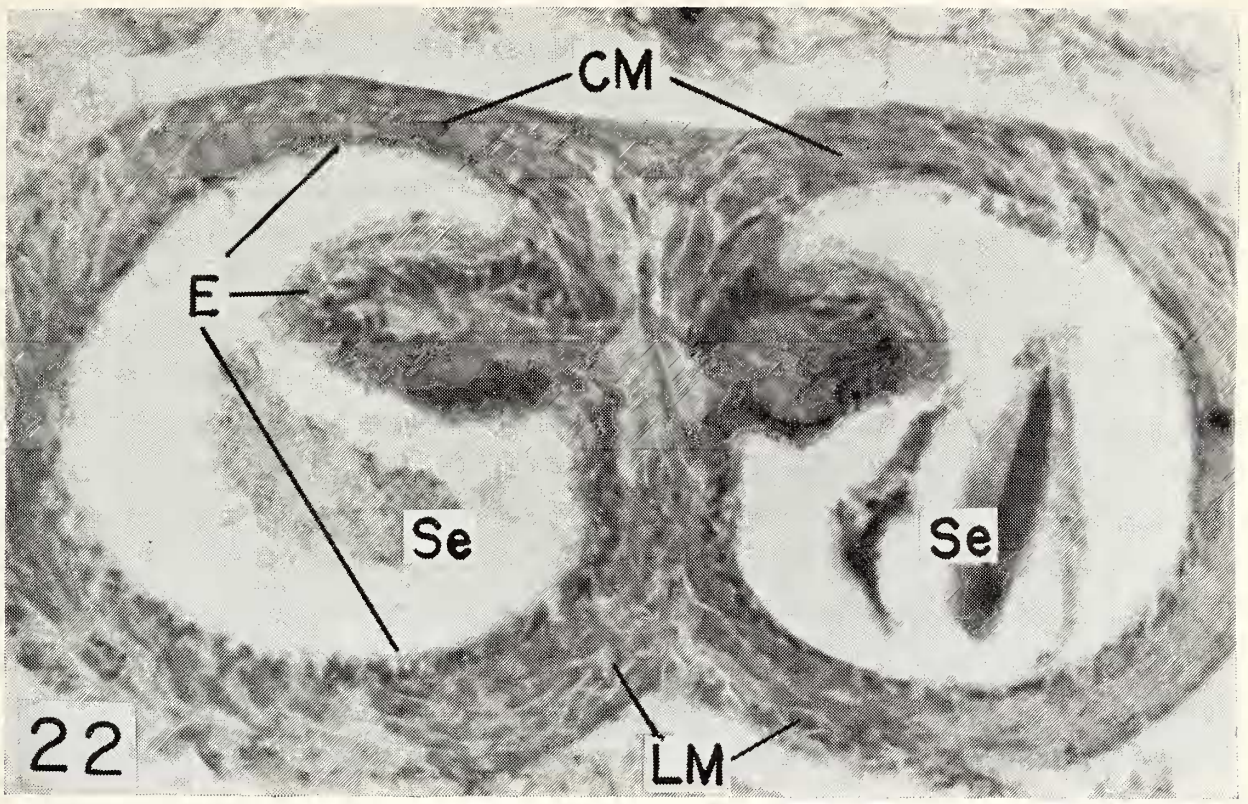
sometimes coiled and convoluted within the lumen. Usually, if the secretion is coiled within the lumen of the gland on one side, it is also coiled within the lumen of the gland on the other side. The muscle fibers surrounding the epithelium of the glands are arranged in two layers, an inner circular layer and an outer longitudinal layer.

The epithelial cells of the accessory gland ducts are generally cuboidal in shape, and they are surrounded by two layers of muscle, an inner circular layer which is four or five muscle fibers in thickness and an outer longitudinal layer which is one or two fibers in thickness (Figs. 20 and 22). The prominent, basophilic secretion of the accessory glands continues into the anterior portion of the accessory gland duct. Some sections show this secretion in the constricted, posterior region of the vas deferens as well as in the accessory gland duct. As the two ducts approach each other, the epithelium of each median wall is raised into a prominent ridge which projects into the lumen of the duct. The epithelium of this ridge is composed of cells which are generally columnar in shape.

The ridge of high columnar cells found on the median wall of each accessory gland duct is still present as these separate ducts are brought together to form the bound accessory gland duct. Muscle fibers are arranged in two layers, an inner circular layer of two or three fibers in thickness which surrounds each duct and an outer circular layer of three or four fibers in thickness which binds the two ducts together (Figs. 22 and 23).

The bound accessory gland duct becomes the ejaculatory duct when the epithelial ridges on the median walls decrease in height and the columnar cells become squamous in shape. The muscle fibers between the adjoining walls of the ducts decrease in number and disappear. The epithelial partition then breaks, and the two lumina form one lumen (Fig. 5). Just before this median wall disappears, the low cuboidal epithelial cells of the mid-region of the lateral walls increase in height, become columnar in shape, and form longitudinal ridges. These lateral ridges continue and project further into the lumen to form two folds of high columnar-shaped cells. On the dorsal wall of the duct and on either side of the remnant of the median wall, the squamous-shaped epithelial cells are somewhat elevated to form two, small, dorsal, longitudinal ridges. The epithelial cells on the ventral wall of the duct are cuboidal and squamous in shape, and they remain so throughout the length of the duct. At the beginning of the ejaculatory duct, a very thin, sclerotized intima lines the epithelium. The muscle coat external to the epithelium consists of a heavy layer of circular fibers and longitudinally arranged fibers within the lateral folds.

The first indication of the wedge in the ejaculatory duct is a thickening of the intima on the dorsal surfaces of the lateral folds (Fig. 6). The arms of the wedge are formed as the lateral margins of this thickened intima are extended dorsally. These arms follow the contour of the dorsolateral walls of the duct and approach the dorsal ridges. These ridges become enlarged, and the lateral



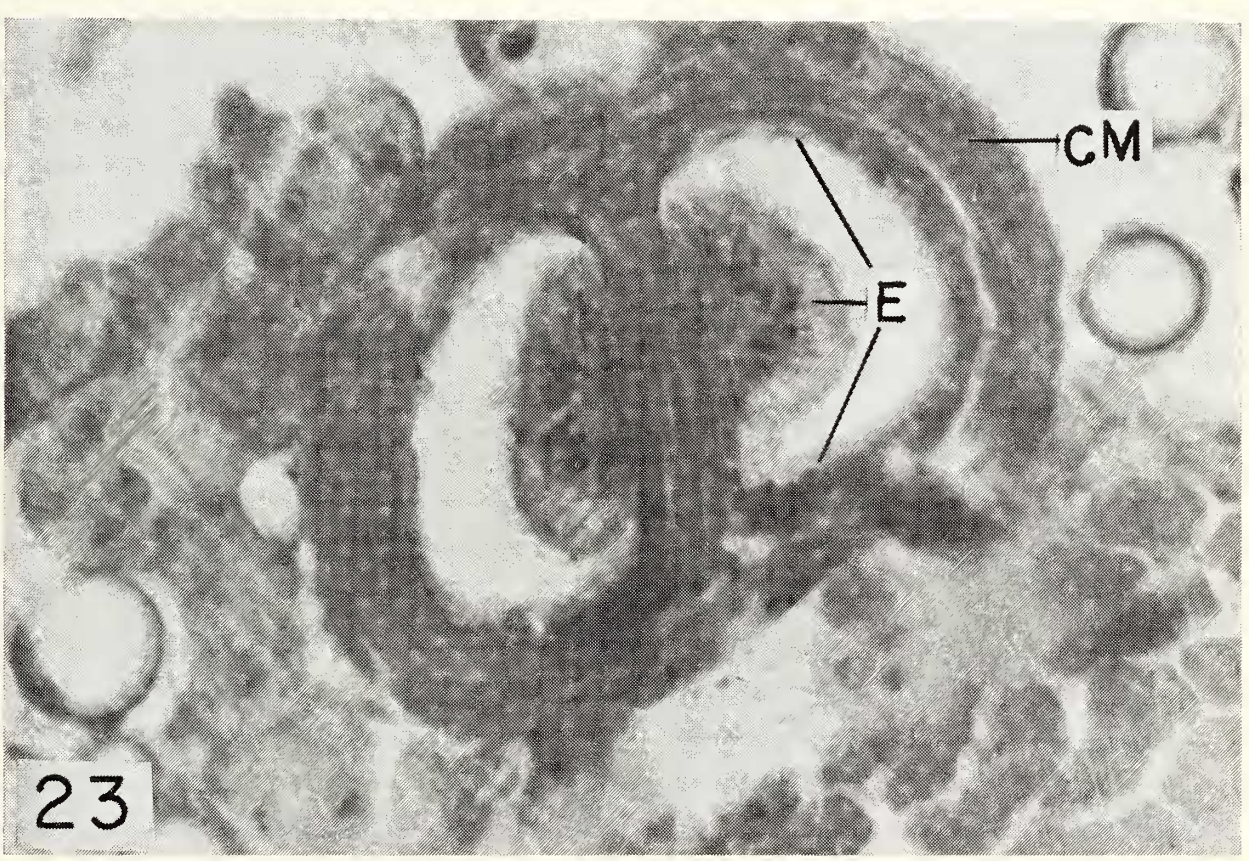


Fig. 22. Photomicrograph of transverse section of accessory gland ducts approaching each other to form the bound accessory gland duct. × 1,935.

Fig. 23. Photomicrograph of transverse section of the bound accessory gland duct. × 1,935.

folds decrease in height. The arms of the wedge increase in thickness and are depressed toward the floor of the duct. Here, sections of the duct show that each arm is U-shaped with the open end of each U facing the other. The inner surfaces of the arms are irregularly grooved. The enlarged dorsal ridges extend downward into the lumen of the duct between the arms of the wedge (Fig. 7). The upper edges of the arms are reflected outward and the lower edges converge and then fuse. As these lower edges converge, each divides to form an upper and lower segment with epithelium between them. The lower segments fuse first, then the upper. The seam is raised and the surface area on either side of the seam is deeply grooved. In the muscle coat, a few longitudinal fibers are concentrated in a thin layer just beneath the epithelium on the floor of the duct and in the dorsal ridges (Fig. 8). The dorsal epithelial ridges become smaller and then disappear (Fig. 9). The lateral margins of the wedge quickly diminish in height, and the floor becomes smooth. The wedge becomes a gutter-like trough, which tapers to a point on the floor of the duct. The epithelial cells of the lateral walls become columnar. Drastic changes occur in the circular fibers of the muscle coat, first on the inside and gradually toward the periphery. These fibers become oblique and then longitudinal in direction. Only a few fibers on the extreme periphery remain oblique or circular (Fig. 10).

The ejaculatory duct extends a short distance beyond the end of the wedge. Its ventral wall becomes thinner and finally disappears as it opens into the dorsoposterior region of the aedeagal bladder. The epithelium of the duct becomes continuous with the epithelium of the bladder, and the longitudinal muscle fibers at its posterior end mingle with the oblique fibers of this region of the bladder.

A cluster of unicellular glands are found above the posterior end of the ejaculatory duct at its junction with the aedeagal bladder (Fig. 15). There are approximately 18 or 20 of these spherical or pear-shaped cells. Each cell has a prominent nucleus which is centrally located within finely granular, acidophilic-staining cytoplasm. A thinly sclerotized duct extends from the lower portion of each cell. Some of these ducts open separately into the lumen, and some combine to form a common duct, which then opens into the lumen.

The aedeagal bladder has a rather thick, wrinkled intima, and the underlying epithelium is composed of flattened cells. The nuclei of these cells can be seen between the folds of the intima (Figs. 5–10). The muscle fibers which surround the bladder are wider in diameter than the visceral muscle fibers which surround the other organs of this reproductive system. Histologically, they have the appearance and texture of body wall muscles. At the anterior end of the bladder, the muscle fibers are longitudinally arranged, and the layer consists of about 12 fibers in thickness. These muscle fibers merge with the numerous fibers within the lamina annularis or the basal ring of the external genitalia. This arrangement of the muscles tends to obscure the outer margin of the aedeagal bladder.

At the posterior end of the bladder, only one or two muscle fibers are present dorsally and dorsolaterally, and they are oblique and longitudinal in direction. These posterior muscles of the bladder are attached to the walls of the inner genitalic valves. Within the aedeagal bladder, particularly at its posterior end, there is a granular, basophilic secretion. The aedeagal bladder opens posteriorly and dorsally between the inner genitalic valves and into the sperm gutters of these valves (Figs. 3, 16, and 17).

DISCUSSION

The testes in *N. harrisi* are small and lie in the posterior region of the third gastral segment. These organs in *E. hamatum* (Forbes, 1958) are large and extend through the first three gastral segments. The testicular follicles in both these males are long, slender tubules, 22–25 in each testis of *N. harrisi* and approximately 20 in each testis of *E. hamatum*. In *D. labiatus* (Mukerjee, 1927), each testis contains "a fair number" of small, tubular follicles.

The common, short duct into which the vasa efferentia open in *N. harrisi* is similar to the reservoir described for *E. hamatum*. In *N. harrisi*, the follicles as well as the vasa efferentia generally contain no spermatozoa, and the histology of the testes indicates that they may be disintegrating. This is to be expected since these males were collected while flying around lights at night. A similar condition of the testes in *Camponotus pennsylvanicus* has been reported (Forbes, 1954).

The position and the shape of the vasa deferentia in *N. harrisi* and in *E. hamatum* are similar, and the arrangement is quite uniform. Although Mukerjee reports that this organ in *D. labiatus* is usually U-shaped, he describes a swelling at its anterior end, the collecting sac, and a larger dilation at its posterior end, the vesicula seminalis. He observed variations in the position and the size of this vesicula seminalis. The vasa deferentia in *N. harrisi* and *E. hamatum* are packed with spermatozoa, and, in *D. labiatus*, spermatozoa are found in the dilated regions of the vas deferens. These organs store the spermatozoa. The lumina of the constricted ends of the vasa deferentia in *N. harrisi* are plugged with a granular, acidophilic material; this condition was also observed in *C. pennsylvanicus*.

A single capsule covers the testes in *N. harrisi*, each testis is covered by a capsule in *E. hamatum*, and no capsule is found in *D. labiatus*. This capsule, in *E. hamatum* and *N. harrisi*, covers all but the last portion of the vas deferens, and in the latter species it is extended anteriorly and is attached to the dorsal diaphragm in the first segment. The slides of the capsule for *N. harrisi* and the illustration for *E. hamatum* (Forbes, 1958, Fig. 4) show similar histological features; this agrees with the report for *C. pennsylvanicus*.

The shape and arrangement of the accessory glands and the accessory gland ducts of *N. harrisi* and *E. hamatum* correspond, while the accessory glands of

D. labiatus are large, slightly curved, thick-walled tubes. The bound accessory gland duct of *N. harrisi* agrees in its histology with that of *E. hamatum*, but anatomically there is a difference. In *E. hamatum*, this duct encircles the ventriculus five or six times. No such arrangement is seen in *N. harrisi*. The bound accessory gland duct in *N. harrisi* is approximately equal to each accessory gland. A similar relationship between the length of the bound accessory gland duct and the accessory glands is found in *E. hamatum*.

The ejaculatory duct in *D. labiatus* is longer than it is for *N. harrisi* and *E. hamatum*. Mukerjee found in one male a single, blind diverticulum arising from the dorsal side of this duct, but no such structure was seen in any specimens of *N. harrisi* or *E. hamatum*.

A sclerotized wedge in the ejaculatory duct has now been described for several male ants; its shape seems to be somewhat different for each species. Clausen (1938) was the first to report this wedge in *Formica rufa*. It has been described in detail for *C. pennsylvanicus* and reported for *E. hamatum*. In this study, this wedge is described for *N. harrisi*. Mukerjee states that there is "a pair of chitinous penes present on its ventral surface near the terminal opening of the duct." Although the histology of this wedge is similar in *N. harrisi* and in *C. pennsylvanicus*, its position in the ejaculatory ducts of each is different. In *N. harrisi*, the wedge arms arise on the lateral folds of the duct, while, in *C. pennsylvanicus*, they arise on ventrolateral folds. There are also differences in the way the arms fuse and in the shape and position of the posterior ends of the wedges.

An aedeagal bladder is present in both *N. harrisi* and *E. hamatum*, but no mention is made of it in *D. labiatus*. However, this organ is easily overlooked since the fibers of its muscle coat are similar to the body wall muscle fibers which fill the lamina annularis where it is located. The aedeagal bladder in *N. harrisi* was first seen in sections of the reproductive system. The secretion in the aedeagal bladders of *N. harrisi*, *E. hamatum*, and *C. pennsylvanicus* is granular and basophilic.

Detailed descriptions and figures of the external genitalia and the two terminal abdominal sternites are included in this study. These agree with the limited descriptions of some of the genitalic valves and the subgenital plate which were made for *N. harrisi* by Borgmeier (1955) in his monumental monograph on the males of Neotropical doryline ants. A description of the eighth sternum of *N. harrisi* has been included since, in a study of some species of the genus *Polyergus*, it was suggested that differences in the shape of this segment might have value in taxonomic designations (Forbes and Brassel, 1962).

The unicellular glands present at the posterior end of the ejaculatory duct in *N. harrisi* have not been reported in the histological studies of other male ants. However, aedeagal glands, which are unicellular, have been observed on the dorsal side of the inner genitalic valves in a few formicine and myrmicine species (Forbes, 1954). These aedeagal glands were not seen in *N. harrisi*.

These comparisons of the male reproductive systems of the doryline ants indicate that *Neivamyrmex* is closer anatomically to *Eciton* than to *Dorylus*.

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abbreviations

A, anus
Aa, aedeagal apodeme
Ab, aedeagal bladder
AD, accessory gland duct
Ad, aedeagus
AG, accessory gland
BD, bound accessory gland duct
C, crop
CA, testicular capsule
Cd, short common duct
CM, circular muscle
DD, dorsal diaphragm
E, epithelium
Ed, ejaculatory duct
F, testicular follicles
G, ganglion
Gc, gland cells
Gr, granular material
H, heart
I, intestine
In, intima
L, lamina aedeagalis
LA, lamina annularis
LM, longitudinal muscle
LP, lamina parameralis
M, malpighian tubules
OM, oblique muscle
Pm, paramere of outer valve
R, rectum
S, spathe
Se, secretion
SG, sperm gutter
Sp, subgenital plate
T, testis
Tr, trachea
tr, tracheoles
V, volsella
Vd, vas deferens
Vn, ventriculus
W, wedge
III–VIII, Roman numerals indicate abdominal segments